

Hand harvesting quickly depletes intertidal whelk populations

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Abstract: With the collapse of the offshore whelk trawl fishery in Georgia, interest has increased in harvesting whelk from inshore areas where trawling is prohibited. This study examines the effects of hand harvesting on local intertidal populations of whelk. Over a 34 day period from 27 February to 1 April 2006, 1,824 whelk were hand harvested at low tide: 91.2% knobbed, *Busycon carica* (Gmelin, 1791); 4.7% lightning, *Busycotypus sinistrum* (Hollister, 1958); 4.1% channeled, *Busycotypus canalicalatus* (Linnaeus, 1758); and one pearwhelk, *Busycotypus spiratus* (Lamarck, 1816). Significantly greater numbers of knobbed and lightning female whelk were found than males. Mean shell lengths for females were consistently larger than males of all species. The study period was divided into three collection periods that were separated by approximately one week. The numbers of whelk harvested and their mean shell lengths significantly decreased between sampling periods as stocks were depleted. All species and sexes were active in both daytime and nighttime; however, significantly more knobbed and channeled whelk were harvested when sampling occurred closer to the middle of the night and significantly fewer toward the middle of the day. Nocturnal feeding is likely a cryptic adaptation to avoid predation and desiccation, and many whelk presumably remain buried on the intertidal flats during diurnal exposure. This study was conducted in the period leading up to copulation and egg-laying on the intertidal sandy-mud flats in inshore areas in coastal Georgia. Nocturnal hand harvesting at this time of the year could very quickly have detrimental impacts to local whelk stocks. Further implications of this work for an intertidal hand harvest supplemental whelk fishery are discussed.

Key words: behavior, whelk, fishery, intertidal, nocturnal

Four species of whelk (Family Melongenidae) occur in the coastal waters of Georgia: the knobbed whelk *Busycon carica* (Gmelin, 1791), the lightning whelk *Busycon sinistrum* (Hollister, 1958), the channeled whelk *Busycotypus canalicalatus* (Linnaeus, 1758), and the pearwhelk *Busycotypus spiratus* (Lamarck, 1816) (Abbott 1974). The first three species are common, while the pearwhelk is rare (Walker 1988). Georgia's coastal water temperatures typically follow a seasonal pattern, ranging from 8-10 °C in winter to 30-32 °C in summer months. Seasonal intertidal whelk abundances have been associated with reproductive and feeding behavior (Magalhaes 1948, Walker 1988, Power *et al.* 2002a, Walker *et al.* 2004, 2008).

The Georgia Department of Natural Resources' Coastal Resources Division first authorized the commercial harvest of whelk in 1980 (Belcher *et al.* 2001). The fishery developed primarily as an offshore winter fishery when shrimpers changed gear, utilizing nets with a larger mesh and heavy chain attached to the bottom edge of the net to enhance bottom harvesting. Whelk landings peaked in 1990 in Georgia, where 462,196 kg of meat valued at \$507,718 was reported (Georgia Department of Natural Resources 2010). The fishery remained viable through the 1990s, but landings began to decrease drastically in 2000. The average annual landings for the period 2004-2008 have been 1,372 kg of meat, valued at \$3,832 (Georgia Department of Natural Resources 2010). The collapse of the trawl fishery led to an increase in price

from \$1.10 per kg in the early 1990s to \$2.72 per kg in 2007, which resulted in mounting interest in harvesting whelk from the inshore areas (typically depths up to 6 m) where trawling is prohibited. Prices have since subsided back to 1990's levels and currently can reach up to \$1.21 per kg.

Blue crab, *Callinectes sapidus*, fishers have been harvesting channeled whelk from inshore waters for years. Georgia crabbers typically soak crab traps baited with Atlantic Menhaden (*Brevoortia tyrannus*) overnight to catch blue crabs. However, Walker *et al.* (2003) determined a combination of fish and crab bait was more effective for directly targeting whelk. Studies have shown that local stocks can be depleted within weeks through pot fishing (Walker *et al.* 2003, Shalack 2007). Most of Georgia's hard clam *Mercenaria mercenaria* (Linné, 1758) (Walker *et al.* 1980, Walker and Rawson 1985) and oyster *Crassostrea virginica* (Gmelin, 1791) (Harris 1980) stocks occur in the intertidal zone. Shellfishermen have traditionally hand gathered knobbed whelk from these intertidal areas (Walker 1988). Commercial clam and oyster fishermen do not currently have a possession limit for hand-harvested whelk from the intertidal zone and may collect year around and at any hour of the day. Licensed recreational fishermen are permitted to take up to 1 bushel of whelk per day.

In previous studies, whelk have been reported to be abundant in the study area during the time of year that this

work was conducted. This period typically leads up to the start of copulation and egg deposition on the intertidal mud flats in early April (Walker 1988, Power *et al.* 2002a). The Georgia coast experiences a semi-diurnal tidal cycle with a tidal range up to 2.3 m. Hand picking of whelk by intertidal clam and oyster fishers would produce large yields at this time of the year, but could have negative impacts on population recruitment. In this study we hand harvested whelk from an intertidal habitat in Georgia to quantitatively describe the whelk community composition, abundance, demographics, and sex ratios with regard to tidal stage, time of day, ambient temperatures (air and water), and moon phase. This information will have value in the management of a sustainable inshore whelk fishery.

MATERIALS AND METHODS

Whelk were hand collected from the intertidal area of Dead Man Hammock, Wassaw Island, Georgia from 27 February to 1 April 2006 (Fig. 1, Appendix 1). Catch per unit effort was defined as the number of whelk captured during each collection period. Given that the same physical area was searched during each low tide, it was determined that the time taken to collect whelk each time was irrelevant.

Harvesting occurred during low tides by walking along the contours of the oyster reefs (approx. 450 m) and searching a 60-m swath of the adjacent mud flat. Harvesting occurred on days that the tide receded enough to permit collecting in the lower intertidal zone. This resulted in three distinct collection periods that were separated by approximately one week over the course of the entire study period. On the first day of collection, harvesting started after the tide had turned; all other collections started with the outgoing tide.

Day collections are defined as occurring between the hours of sunrise and sunset. The time of day for each collection was further defined by dividing both the day and night into eight light intensity intervals. Four equal quarters were established from sunrise to the middle of the day and were ranked from 0 to 4, while the four subsequent quarters to sunset were ranked from 4 to 0. Likewise the quarters from sunset to the middle of the night were ranked from 0 to -4 and from -4 to 0 for the quarter to sunrise. The light intensity was determined by averaging the score of the intervals during which each collection occurred. The extent of the tidal cycle was defined by the mean lower low water (MLLW) reported by NOAA (tidesandcurrents.noaa.gov) for the study site. The lunar phase was also recorded for each night time collection by recording the percentage of the moon visible as reported by the US Naval Observatory (www.usno.navy.mil). Surface water and air temperatures were taken with a thermometer on site during collections.

Harvested whelk were returned to the laboratory, where they were held in separate raceways until they could be identified to species and measured for shell length (siphonal canal to shell apex). Each whelk was identified by super gluing an identifying Hallprint® plastic tag to the body whorl near the top of the aperture. Tagged whelk were then relaxed in seawater containing 7% magnesium chloride and sex was determined by the presence or absence of a penis. In this region, imposex is not a commonly observed phenomenon in these species. Whelk recovered completely after sexing but were not released until the study was completed to avoid recapture and confounding the impacts of hand-harvesting fishing pressure.

Size frequency distributions were plotted for male, female, and unsexed knobbed whelk for each of the three collection periods and for the entire collection period. Since fewer channeled and lightning whelk were harvested, combined size frequency distributions for all collection periods were only plotted for these species. A goodness-of-fit *G*-test was calculated for the number of males to females across these categories to identify those

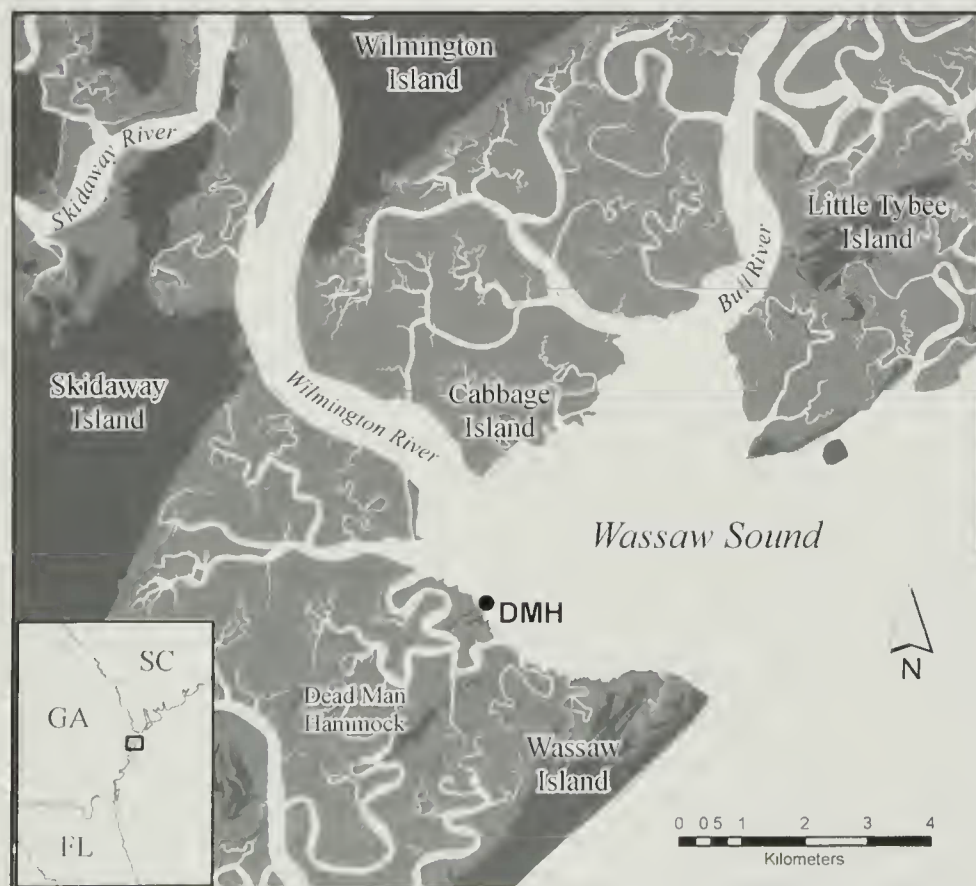


Figure 1. Dead Man Hammock study site on Wassaw Island, Georgia (31°55'11"N 80°58'19"W).

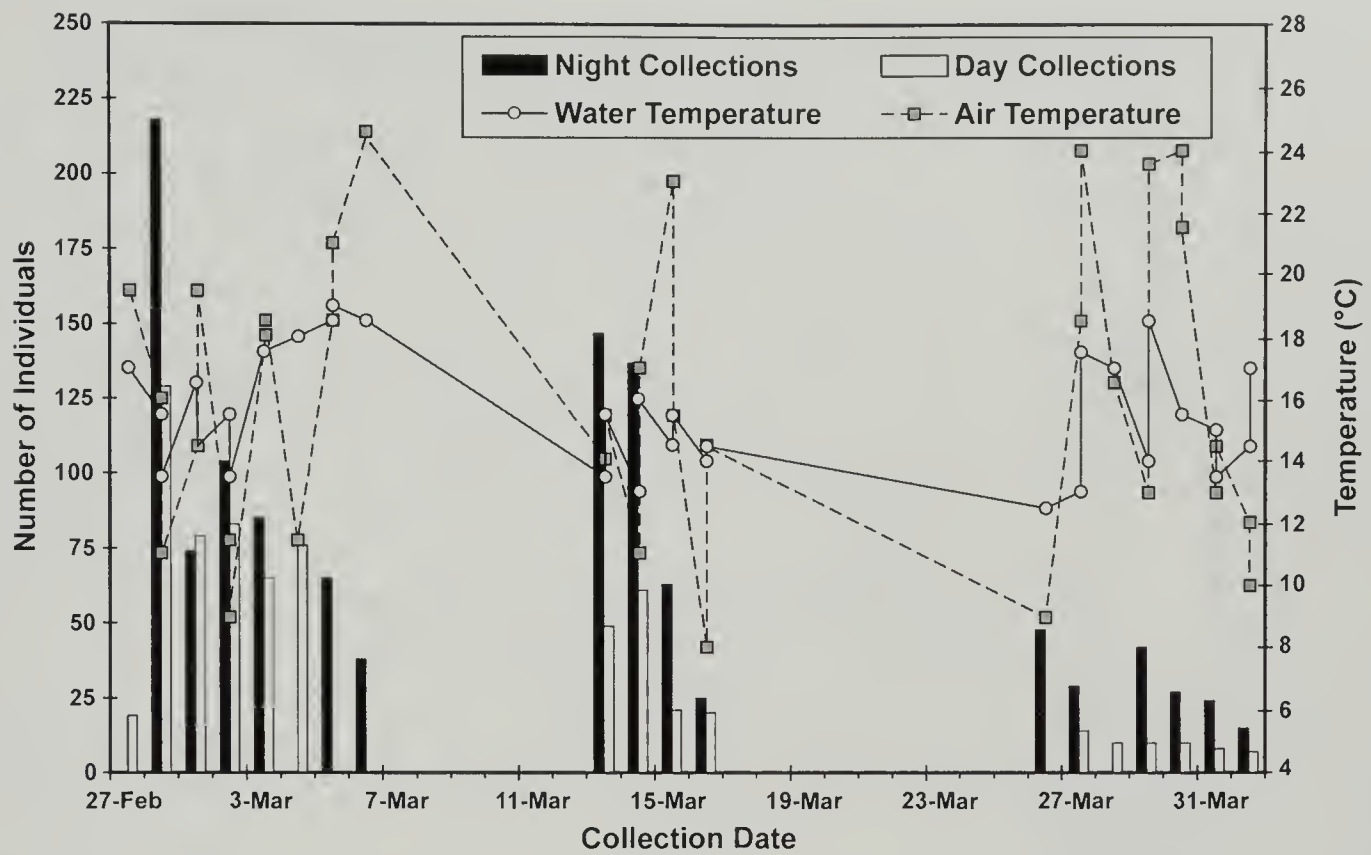


Figure 2. The number of diurnal and nocturnal whelks harvested over the three collection periods between Feb. 27 and Apr. 1 and the corresponding on-site ambient water and air temperatures (°C).

collections significantly different from a 1:1 ratio. Only one male lightning and one pear whelk were identified and, therefore, were excluded from this analysis. ANOVAs were used to test for significant differences between the numbers of each whelk species captured during daylight versus during

the night (SAS Institute Inc. 2008). A factorial two-way ANOVA was used to compare the mean sizes of male and female knobbed whelk captured during daylight versus night hours (SAS Institute Inc. 2008). Spearman's rank correlation analysis was used to determine significant correlations

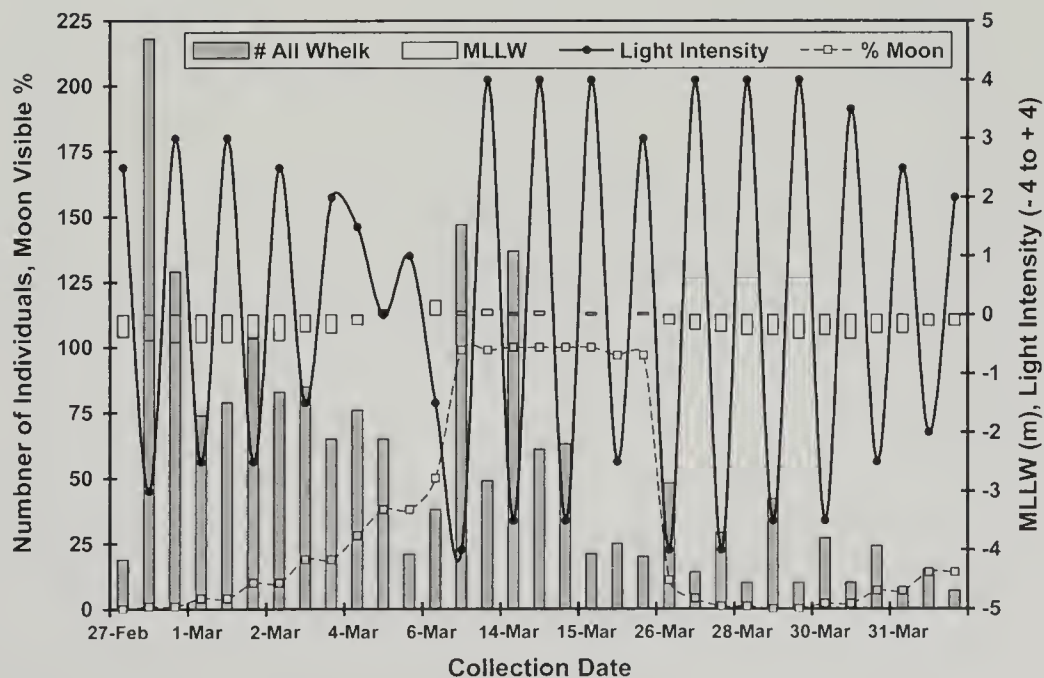


Figure 3. The number of whelk individuals collected in relation to date, tide (mean lower low water), light intensity (-4 to +4), and lunar phase (0 to 100%).

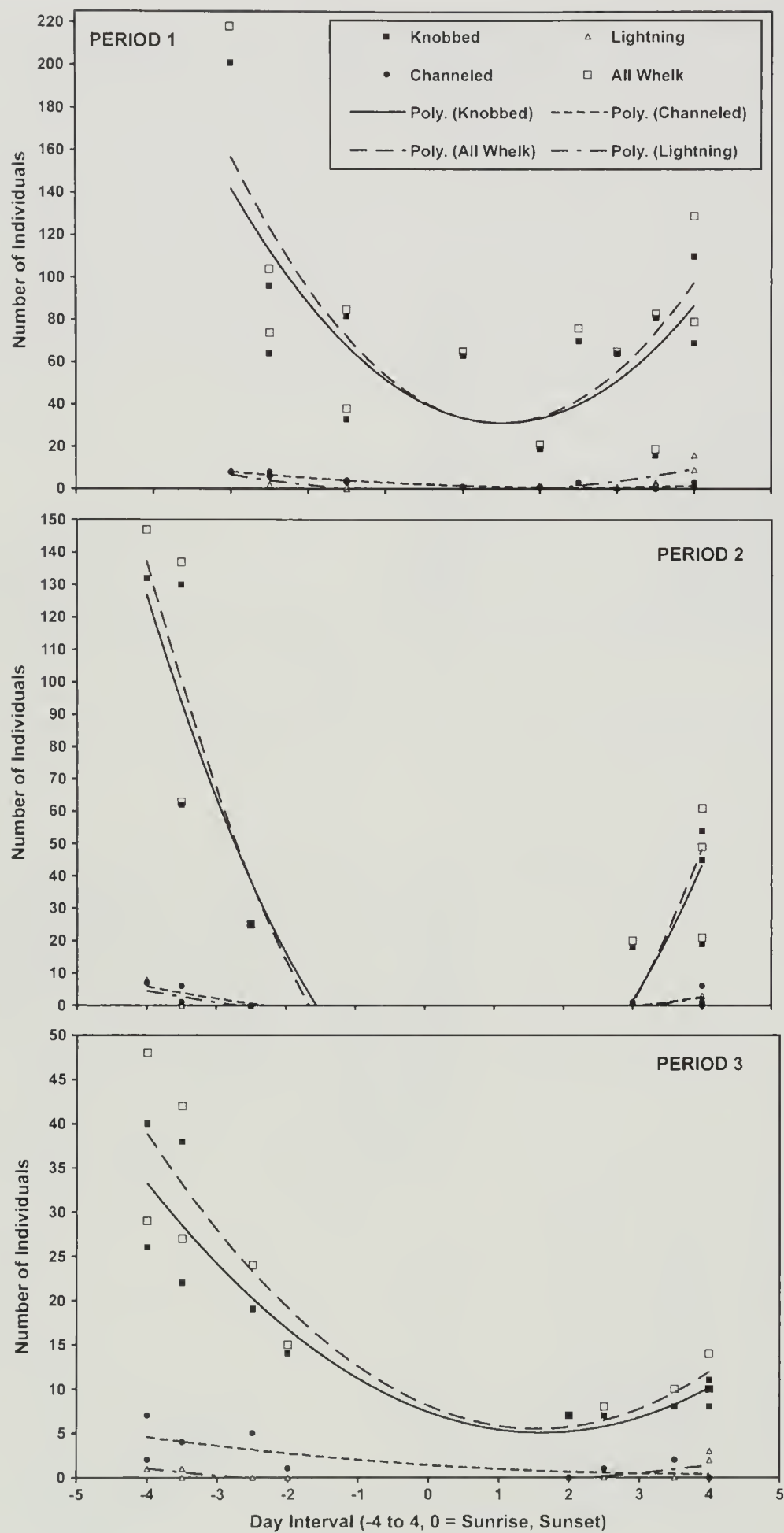


Figure 4. The numbers of individual knobbed, lightning, channeled, and all whelks harvested during the three collection period (Feb. 27 to Mar. 06, Mar. 13 to Mar. 16, and Mar. 26 to Apr. 1) in relation to the mean collection time light intensity (-4 to +4).

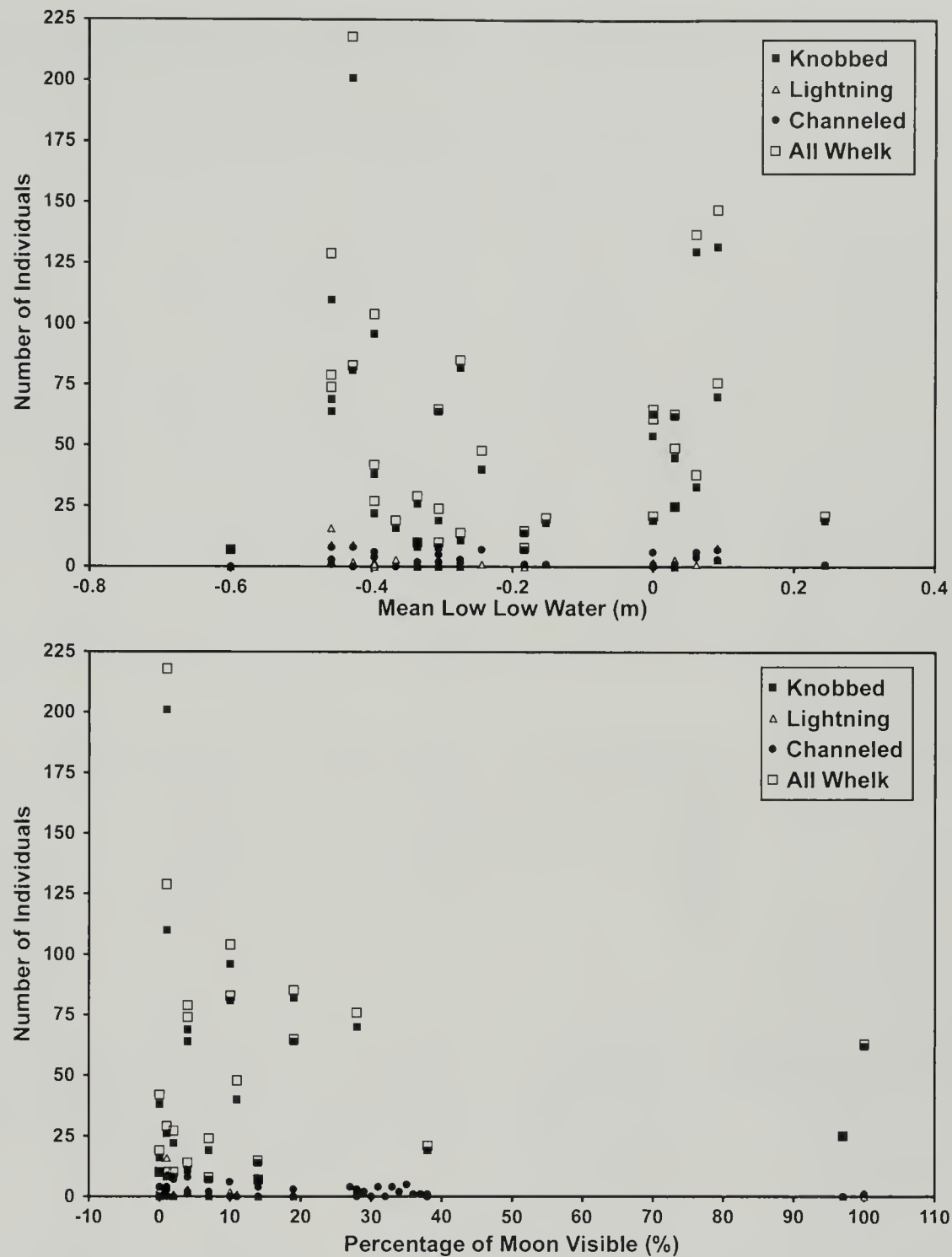


Figure 5. The numbers of individual knobbed, lightning, channeled, and all whelks harvested during the three collection periods (Feb. 27 to Apr. 1) in relation to the extent of the tidal stage as defined by mean lower low water from NOAA (upper panel) and in relation to the lunar phase as quantified by the percentage of the moon visible by the US Naval Observatory (lower panel).

between the numbers, sizes, and sexes of whelk and the corresponding tidal height, time of day, moon phase, and air and water temperatures. Polynomial and linear trend lines were fitted using Excel to further explore the relationships between the various parameters and changes in whelk species abundances over the study period. An ANOVA and an ANCOVA (using light intensity as a covariate) were also used to determine the significance of changes in the numbers of whelk captured between the three sampling periods (SAS Institute Inc. 2008).

RESULTS

Water and air temperatures were typical of coastal Georgia during the study period (Fig. 2). Water temperatures ranged from 13 to 19 °C during daylight collections and from 12.5 to 18.5 °C during night collections. Daytime aerial temperatures ranged from 11.5 °C to 24.5 °C and nighttime aerial temperatures from 9 °C to 18.5 °C. Day length increased from 11 hours 27 minutes to 12 hours and 31 minutes over the course of the study period, which consisted

Table 1. Spearman’s rank correlations for (a) numbers of all whelks, (b) mean shell lengths (SL) of sexed knobbed whelks, and (c) mean shell lengths of sexed lightning and channeled whelks. Correlations are provided for: sample sizes, male to female ratios, mean shell lengths, mean lower low water (MLLW), percentage of moon visible (for collections with mean light intensities 0 to -4), water and air temperatures, and the mean light intensity interval recorded during each collection for all samples. Only one male lightning whelk was identified and is not included in (c). Significant correlations at $P < 0.05$ are indicated with an * and in boldface font.

(a)	Knobbed (#)	Channeled (#)	Lightning (#)	All whelk (#)
Mean shell length	0.34*	-0.15	0.35	0.56*
MLLW	-0.05	0.01	-0.17	-0.06
% Moon visible	0.23	-0.29	-0.31	0.22
Water temperature	-0.16	-0.20	-0.40*	-0.17
Air temperature	-0.24	-0.33	0.01	-0.24
Light intensity	-0.40*	-0.59*	0.19	-0.41*

(b)	All knobbed (SL)	Male knobbed (SL)	Female knobbed (SL)
Numbers	0.34*	0.60*	0.22
M:F ratio	-0.63*	-0.59*	-0.30
MLLW	-0.30	-0.31	-0.35*
% Moon visible	-0.07	0.39	0.04
Water temperature	-0.40*	-0.07	-0.26
Air temperature	-0.01	0.03	0.01
Light intensity	0.18	-0.03	0.24

(c)	All lightning (SL)	Female lightning (SL)	All channeled (SL)	Male channeled (SL)	Female channeled (SL)
Numbers	0.35	-0.58*	-0.15	-0.03	-0.35
MLLW	-0.27	-0.53*	0.30	0.25	0.14
% Moon visible	-0.78*	-0.60	0.34	0.73*	0.46
Water temperature	-0.22	-0.64*	0.02	0.09	0.33
Air temperature	-0.02	-0.39	-0.14	0.15	0.25
Light intensity	-0.08	-0.45	-0.11	0.18	0.18

of three discrete sampling periods separated by approximately one week. Collections occurred throughout the range of light intensity intervals established (-4 to +4, Figs. 3-4) and during tides ranging from -46 to 24 cm (Fig. 5). Nighttime collections occurred from new (0%) to full (100%) moons, but no collections occurred between the range of 40 and 90% (Fig. 5).

A total of 1,824 whelk were gathered by hand at Dead Man Hammock on Wassaw Island, Georgia from 27 February 2006 to 1 April 2006. There was a significant difference between the number of each species harvested (ANOVA, $F = 25.56$, $P < 0.01$). Most whelk (91.2%) were knobbed (*Busycarca*), with 4.7% being lightning (*Busycotypus sinistrum*) and 4.1% channeled (*Busycotypus canalicalatus*). Only one pearwhelk (*Busycotypus spiratus*) was found. The numbers of whelk captured at night (- light intensity) versus during the day (+ light intensity) was significant only for channeled whelk (ANOVA, $F = 14.71$, $P < 0.01$). Spearman’s rank correlation coefficients did, however, determine a significant negative association between the mean light intensity interval and the number of knobbed ($R = -0.40$), channeled ($R = -0.59$), and all whelk ($R = -0.41$) at $P < 0.05$ (Table 1).

Table 2. Equations of polynomial lines ($y = ax^2 + bx + c$) fitted to Figs. 4-6 to describe the numbers of individual knobbed, lightning, channeled, and all whelks harvested during each collection period in relation to the mean collection time light intensity.

Period 1	a	b	c	R^2
Knobbed	8.99	-9.23	33.58	0.50
Channeled	0.37	-1.11	1.48	0.85
Lightning	1.06	0.45	-1.52	0.60
All	10.42	-9.89	33.53	0.53

Period 2	a	b	c	R^2
Knobbed	7.48	-10.47	-34.41	0.77
Channeled	0.48	-0.40	-3.39	0.42
Lightning	0.47	-0.26	-4.11	0.44
All	8.43	-11.14	-41.92	0.76

Period 3	a	b	c	R^2
Knobbed	0.89	-2.89	7.38	0.84
Channeled	0.07	-0.52	1.40	0.62
Lightning	0.12	0.05	-0.69	0.40
All	1.08	-3.36	8.09	0.84

The numbers of individual knobbed, lightning, channeled, and all whelk harvested during each of the three collection periods, and according to the day interval in which collection occurred is illustrated (Fig. 4). Polynomial lines and equations (Table 2) are also provided to describe the data. Fewer whelk per collection period were harvested closer to the middle of the day and *vice versa* for night collections. The abundance of lightning whelk was negatively correlated ($P < 0.05$) with water temperature ($R = -0.40$). The extent of tidal height had no significance on the abundances of any of the whelk species.

The sex ratios and size frequency distributions for male and female whelk collected during each period and for the entire collection period are summarized (Table 3) and illustrated (Fig. 6). Given the low numbers of channeled and lightning whelk, only cumulative histograms are presented for these species (Fig. 7). Knobbed whelk ranged in size from 39 to 234 mm, lightning from 82 to 229 mm, and channeled from 50 to 141 mm. Females dominated the larger size classes for all whelk. For knobbed whelk, females (mean = 126.9 mm) were significantly larger than males (mean = 87.4 mm)

at $P < 0.01$. Significantly larger-sized knobbed specimens were also found at night (ANOVA, $F = 9.79$, $P < 0.01$); females collected during the day averaged 121.2 mm, females collected at night averaged 132.7 mm, males collected during the day averaged 86.4 mm, males at night averaged 88.3 mm. Shell length was significantly ($P < 0.05$) and positively correlated with sample size for all whelk ($R = 0.56$), all knobbed ($R = 0.34$), and male knobbed whelk ($R = 0.60$), but was negatively correlated with sample size of female lightning whelk (-0.58). Female knobbed and lightning whelk sizes were negatively and significantly ($P < 0.05$) correlated with MLLW ($R = -0.35$ and -0.53), indicating that lower tides resulted in harvesting larger specimens. Male channeled whelk were positively correlated ($R = 0.73$) with the percentage of the moon that was visible, but lightning whelk were negatively correlated ($R = -0.78$). Finally, the mean shell length of all knobbed and female lightning whelk was significantly and negatively correlated with water temperatures ($R = -0.40$ and -0.64 , respectively).

The male to female ratio for knobbed whelk ranged from 0 to 1.33, and females dominated most samples for each species

Table 3. Number, mean shell length (mm $\pm$ SE), and male to female ratio of four whelk species collected during the entire study period and separately by each collecting period. Period 1 was February 27 – March 06, Period 2 was March 13 – March 16, and Period 3 was March 26 – April 01. Not all specimens were sexed. Only one pearwhelk measuring 85 mm was found. A goodness-of-fit G-test was calculated for the number of males to females to identify those significantly different from a 1:1 ratio (*, $P < 0.05$; **, $P < 0.01$).

	Total	Period 1	Period 2	Period 3
Knobbed whelk				
Number	1,663	968	485	210
All shell length	121.59 $\pm$ 0.79	129.58 $\pm$ 1.00	111.70 $\pm$ 1.33	107.61 $\pm$ 2.28
Female shell length	131.29 $\pm$ 0.86	136.65 $\pm$ 1.00	121.44 $\pm$ 1.72	116.25 $\pm$ 2.96
Male shell length	87.80 $\pm$ 0.79	91.24 $\pm$ 1.09	87.69 $\pm$ 1.22	82.29 $\pm$ 2.06
M:F sex ratio	0.24**	0.19**	0.33**	0.38**
Channeled whelk				
Number	86	38	22	26
All shell length	81.62 $\pm$ 1.88	81.08 $\pm$ 2.92	83.86 $\pm$ 3.55	80.50 $\pm$ 3.48
Female shell length	91.62 $\pm$ 2.99	90.22 $\pm$ 3.73	101.25 $\pm$ 4.84	89.71 $\pm$ 7.36
Male shell length	86.15 $\pm$ 2.72	88.62 $\pm$ 3.12	86.20 $\pm$ 8.91	83.29 $\pm$ 3.69
M:F sex ratio	0.69	0.44*	1.25	1.00
Lightning whelk				
Number	75	50	16	8
All shell length	153.17 $\pm$ 3.59	156.46 $\pm$ 4.55	146.44 $\pm$ 6.80	154.62 $\pm$ 8.10
Female shell length	152.38 $\pm$ 3.88	155.52 $\pm$ 4.63	136.62 $\pm$ 7.04	151.20 $\pm$ 11.45
Male shell length	82.00 $\pm$ 0.00	82.00 $\pm$ 0.00		
M:F sex ratio	0.02**	0.02**	0*	0*
All whelk species				
Total number sexed	1,528	995	358	175
Number females	1,235	839	269	127
Number males	293	156	89	48
M:F sex ratio	0.24**	0.19**	0.33**	0.38**

harvested. The male to female ratio for all whelk and knobbed whelk was 0.24, and for lightning whelk was 0.02 (Table 3), all of which were significantly different from a 1:1 ratio ($P < 0.01$). The male to female ratio for all channeled whelk was 0.69, which was not significantly different from parity. Given that females dominated the larger size categories it was not surprising that the male to female ratio was inversely correlated to shell length for all knobbed and male knobbed whelk ($R = -0.63$ and -0.59).

The sex ratio and size structure of the intertidal whelk population changed over the course of the three collection periods with a general trend of increasing males and smaller sizes and numbers caught as harvesting progressed (Table 3). Given the small sample sizes of channeled and lightning whelk, they were excluded from detailed analysis. There was a significant difference in the mean number of all whelk caught per sampling trip between the three sampling periods ($P < 0.001$), declining from 86.4 to 65.4, and finally 20.3. Similarly, the mean number of knobbed whelk was statistically different between periods ($P < 0.001$) and ranged from 79.33 to 17.25. ANCOVAs between

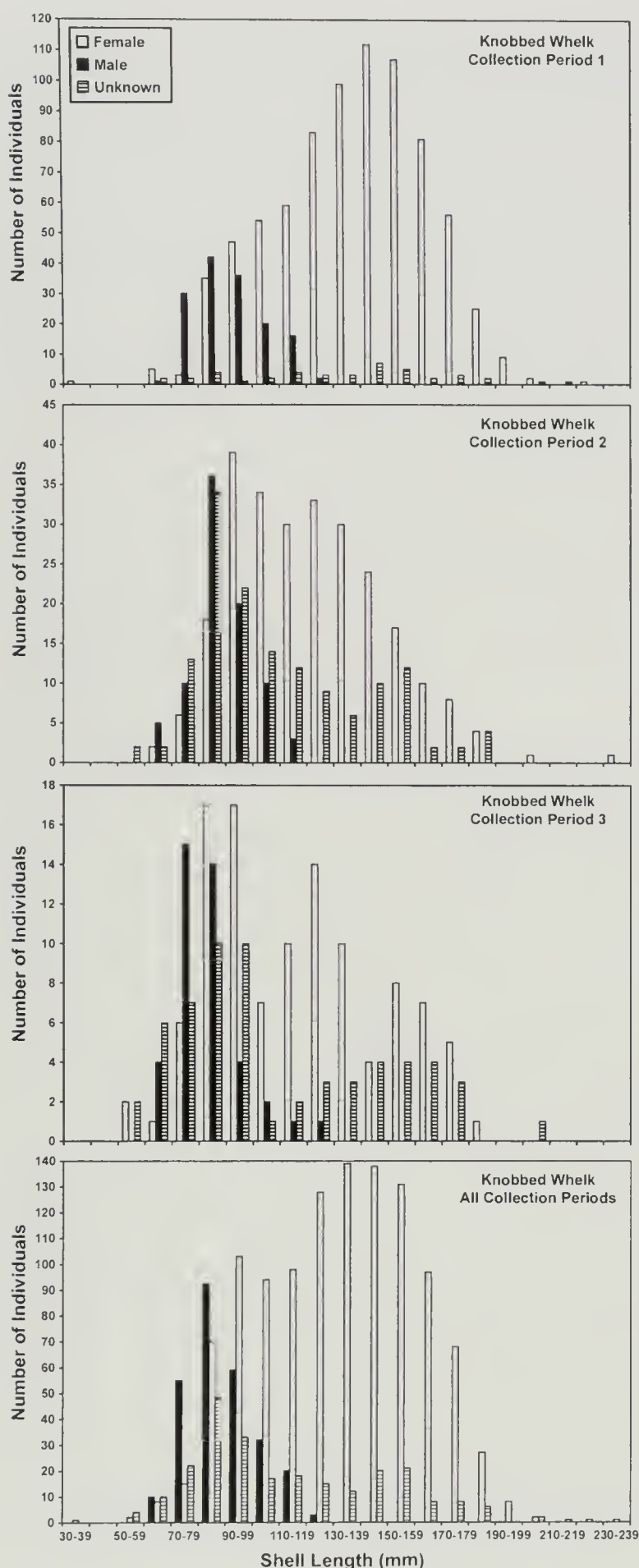


Figure 6. Size frequency distributions (shell length in mm) for male, female, and unsexed knobbed whelks harvested during the three collection periods (Feb. 27 to Mar. 06, Mar. 13 to Mar. 16, and Mar. 26 to Apr. 1) separately and combined.

sampling periods, using light intensity as a covariate, detected significant differences for the mean numbers caught for all whelk ($P < 0.05$) and knobbed whelk ($P < 0.001$) categories. The total number of knobbed whelk collected during the second and third harvesting periods was 50.10% and 21.69% of the first periods catch. Over a period of approximately one month, the whelk catch per unit effort decreased by 78.31%. The mean number of knobbed whelk harvested per event during the first sampling period was 74.5 and decreased to 17.5 in the third period. ANCOVAs were run between sampling periods using light intensity as the covariate, and significant differences ($P < 0.001$) were detected for the mean numbers caught for all whelk and knobbed whelk. Knobbed male to female ratios increased from 0.19 to 0.38 through the three collection periods, but remained significantly different from a 1:1 ratio ($P < 0.01$).

At the termination of sampling, the last five diurnal harvesting events returned ten or fewer whelk on each occasion. Within two weeks our nocturnal efforts would similarly have declined (Fig. 8). The decrease in the catch per unit effort of all and knobbed whelk according to night and day intervals is charted (Fig. 9). The changes in the mean number of individuals for the night and day intervals corresponds to the quadrants from sunrise and to sunset (0 to +2), from sunset and to sunrise (0 to -2), and those representing the middle of the day (+2 to +4) and the middle of the night (-2 to -4). The fastest rate of reduction was observed for the middle of the night samplings, followed by the middle of the day, and then the hours both before sunrise and after sunset, and finally the hours after sunrise and before sunset (Table 4). We estimate that in coastal Georgia, an intertidal whelk population inhabiting an approx. area of 2.4 ha (450 m $\times$ 60 m) can be completely fished out in about six weeks.

DISCUSSION

Previous studies have also documented dominance by the knobbed whelk in the inshore waters of Georgia and South Carolina (Anderson *et al.* 1985, Power *et al.* 2002a, Walker *et al.* 2008). Similar to most sexually dimorphic, commercial whelk species, female whelk at Dead Man Hammock attained a larger size than males in all species (MacIntosh and Paul 1977, Anderson *et al.* 1985, Kideys *et al.* 1993, Castagna and Kraeuter 1994, Power and Keegan 2001, Bruce *et al.* 2006, Walker *et al.* 2008, Power *et al.* 2009). Our data also support previous findings in Wassaw Sound for the size ranges of the various species of whelk in intertidal habitats, and rank them from largest to smallest as follows: lightning, knobbed, channeled, and pear (Walker *et al.* 2008). Our sample size of lightning whelk was small; however, these snails appeared to exhibit a smaller size than those from the

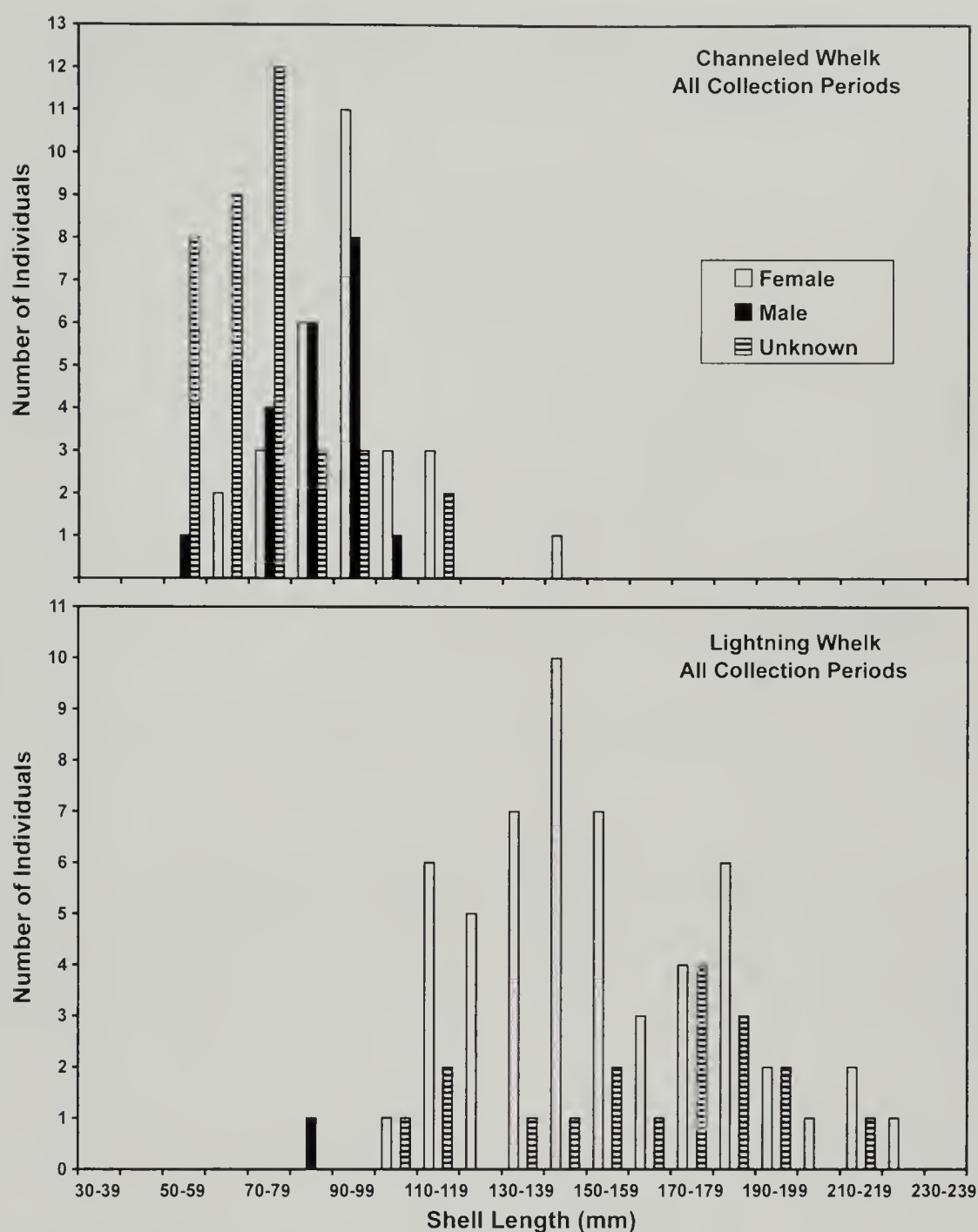


Figure 7. Size frequency distributions (shell length in mm) for male, female, and unsexed channeled and lightning whelks harvested during the three collection periods (Feb. 27 to Apr. 1).

Gulf Coast of Florida (Menzel and Nichy 1958, Kent 1983), supporting Berlocher's (2000) theory of distinct subspecies or unresolved species between the South Atlantic coast and the Gulf of Mexico. In agreement with other studies, the whelk species on Dead Man Hammock were also heavily dominated by females (Power *et al.* 2002b, Walker *et al.* 2008). Our male to female ratios mirror those reported by Walker *et al.* (2008), with the fewest males occurring in lightning whelk, more males in knobbed whelk, and the most males occurring in channeled whelk, though never approaching parity.

Higher abundances of whelk in intertidal habitats in spring and fall in the southeastern United States have been

attributed to migrations to and from subtidal waters; periods of quiescence in the summer and winter suggest whelk are largely buried on the sand/mud flats (Magalhaes 1948, Walker 1988, Walker *et al.* 2004, Shalack 2007). Oysters and clams are the most important prey species for the dominant intertidal species, the knobbed whelk (Carriker 1951, Paine 1962, Davis 1981, Walker 1988, Ferner and Weissburg 2005, Shalack 2007, Walker *et al.* 2008). These bivalves occur predominantly in the intertidal creeks and sounds in coastal Georgia (Harris 1980, Walker and Tenore 1984). During the winter and summer months, environmental conditions in the exposed intertidal zone are extremely harsh, which may reduce feeding rates. The

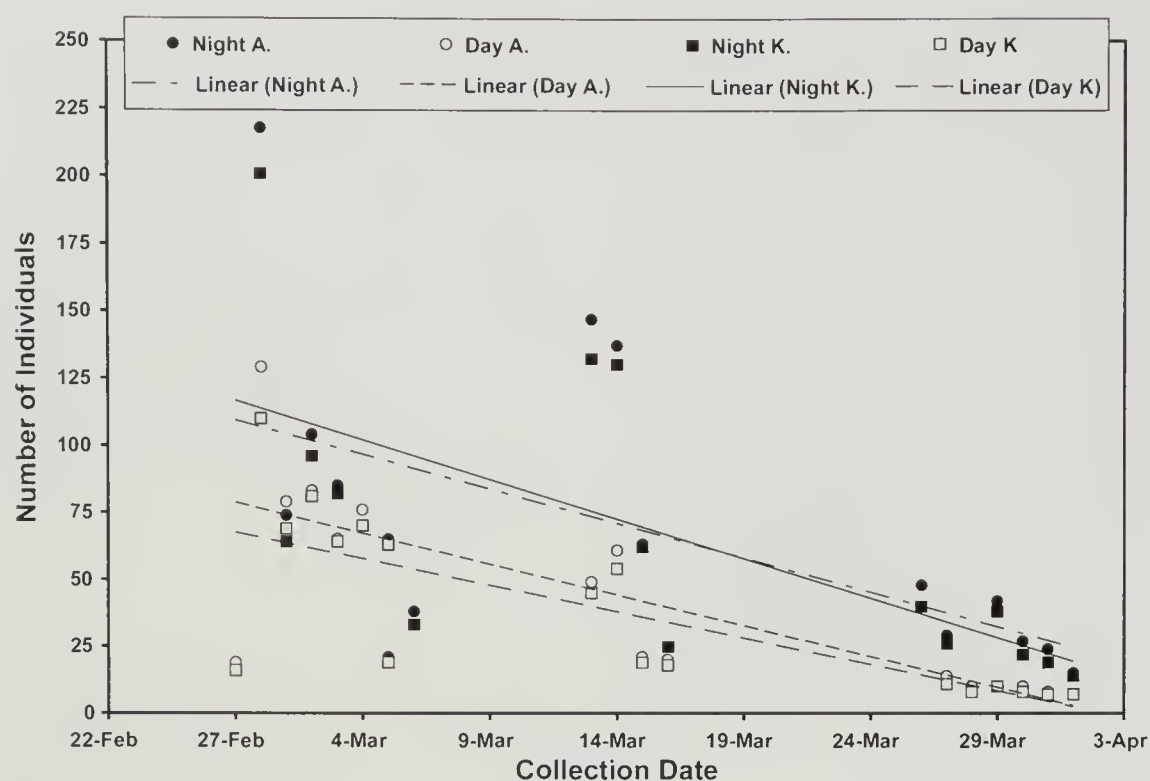


Figure 8. The reduction in the nocturnal and diurnal catch per unit effort for all intertidal whelks and specifically for knobbed whelk over the entire study period (Feb. 27 to Apr. 1). Nocturnal collections occurred between sunset and sunrise.

knobbed whelk has been observed to bury in place and remain inactive at temperatures below 14 °C (Walker *et al.* 2004), and it is likely that similar behavior occurs when excessive temperatures could cause desiccation. Polites and Mangum (1980) noted channeled whelk sluggishness at temperatures greater than 24 °C. Ferner and Weissburg (2005) have observed knobbed whelk feeding on clams and oysters at night in August, but noted their complete absence during the day.

Whelk are readily observed feeding, copulating, and egg laying on these same flats during diurnal low tide exposures in the spring and fall. In Georgia, male knobbed whelk become sexually mature at 85-90 mm, or four years of age, and approx. 100 mm or six years when female (Power *et al.* 2009). Sex ratios can vary geographically and seasonally (Magalhaes 1948, Weinheimer 1982, Anderson *et al.* 1985, Castagna and Kraeuter 1994, Eversole *et al.* 2008, Walker *et al.* 2008). Fertilization in all species is internal after multiple matings, and direct development to juveniles measuring 3 to 7 mm is completed in weeks to months within egg capsules attached along an egg-case string (Castagna and Kraeuter 1994, Power *et al.* 2002a). Anchored strings from all species have been documented from Georgia's intertidal sandy mud flats and subtidal waters in both spring and fall months (Walker 1988, Power *et al.* 2002a, 2009, Walker *et al.* 2008). It is doubtful, given energetic requirements, whether the same females spawn in both seasons.

Given the limited mobility of knobbed whelk (Magalhaes 1948, Ferner 2006, Shalack 2007, Walker *et al.* 2008), intertidal

populations are probably localized and remain year around, but confine feeding during warmer summer and colder winter months to the high tide stage and night time. Spring and fall provide the optimal exposure conditions, which may control reproductive cycles since the deposition of eggs strings can take many days and tidal cycles to complete (Power *et al.* 2002a). These same factors may explain the diurnal and nocturnal abundance patterns observed for knobbed and channeled whelk in the present study: whelk were most active at night (or high tide), but also emerged during diurnal exposure, due to the time of year. Different diurnal behavior patterns have also been reported for whelk from other geographical areas. Magalhaes (1948) found channeled whelk from North Carolina to be more active at night and Paine (1962) reported that pearwhelk actively fed at night in the laboratory. We did not identify any relationship between light intensity and lightning whelk abundance, which corroborates findings from Florida where they are more common and active at all hours (Paine 1962, Kent 1983). Lightning whelk have the largest shells and therefore may be less vulnerable to predation and desiccation than the knobbed, channeled, or pear whelk.

Hand harvesting rapidly reduced the mean size and depleted the numbers of whelk in the study area. We estimate that hand harvesting could remove whelk stocks from a sand/mud flat of approx. 2.4 ha in as short a time as six weeks during a period when whelk activity is at its peak. Therefore, we conclude that a commercial fishery would not be

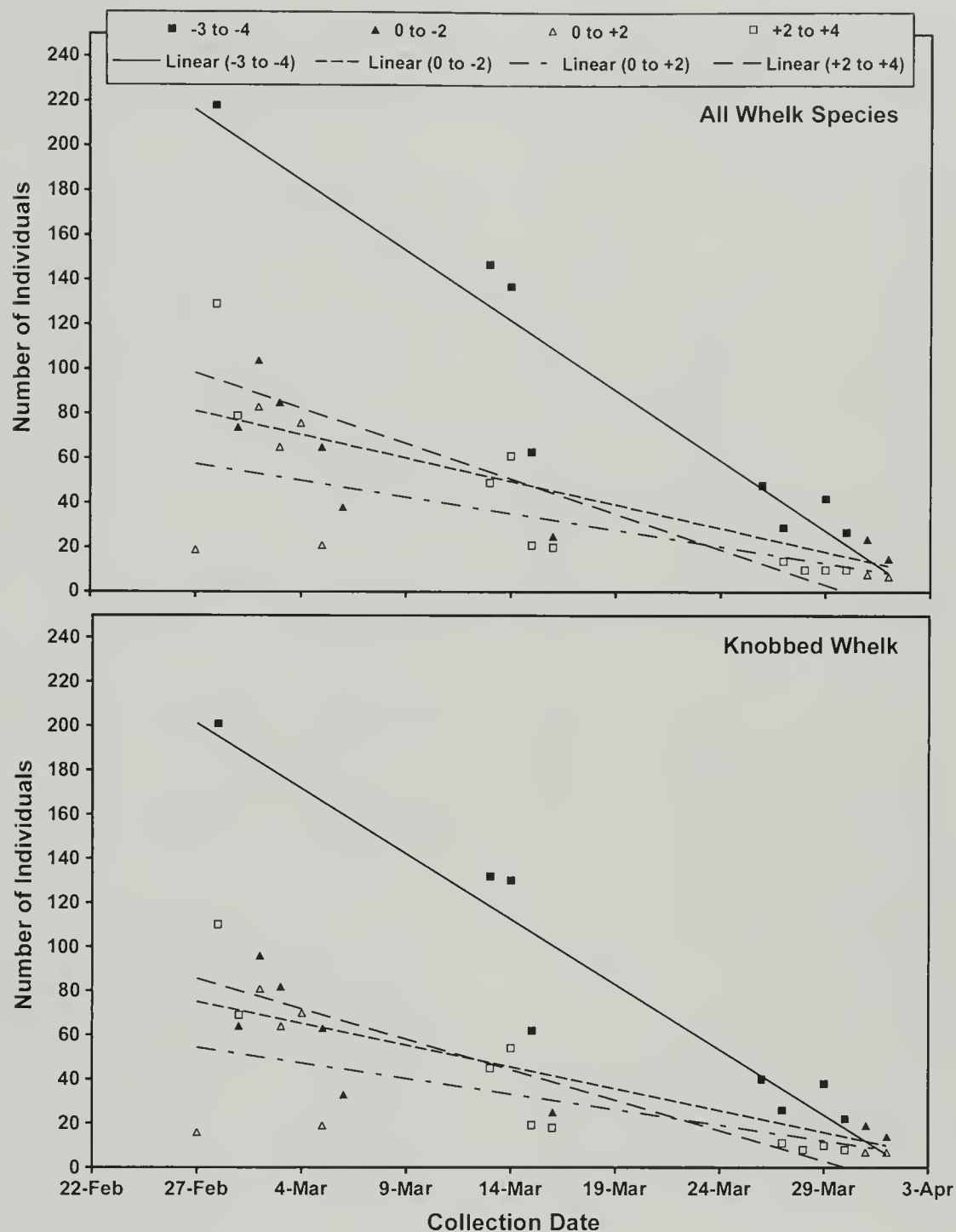


Figure 9. The reduction in the catch per unit effort for all intertidal whelks and specifically for knobbed whelk, according to the mean number of individuals for the day intervals. Day intervals correspond to the quadrants from sunrise and to sunset (0 to +2), from sunset and to sunrise (0 to -2), and those representing the middle of the day (+2 to +4) and the middle of the night (-2 to -4).

sustainable for very long in intertidal locations. In addition, these periods of peak abundances also coincide with the time leading up to the spawning season. While whelk could be very efficiently captured in a seasonal, night-based hand picking fishery, this would predominantly remove large females from the population before they could reproduce and would have detrimental impacts on recruitment to local populations. Whelk have limited mobility and grow slowly (Kraeuter *et al.* 1989, Walker *et al.* 2008), mature at a late age (Power *et al.* 2009), and have low juvenile hatching rates (Power *et al.*

2002b), making them particularly vulnerable to over-exploitation. The gathering of blue crabs, hard clams, oysters, and penaeid shrimp is prohibited by Georgia Department of Natural Resources at night to prevent poaching from non-approved areas, and we suggest this restriction should be applied to protect intertidal whelk populations during the spring and fall months. As an alternative to being closed completely during these months, the enforcement of a catch limit would greatly benefit the sustainability of resources. Outside of the spawning seasons, the catch per unit effort

Table 4. Equations of lines ($y = ax + c$) fitted to Figs. 8 and 9 to describe the decrease in numbers of individual knobbed and all whelks harvested over the study period in relation to the collection time of day. Time of day is expressed as night or day and also in terms of quadrants (from sunrise and to sunset, 0 to +2; from sunset and to sunrise, 0 to -2; and those representing the middle of the day, +2 to +4, and the middle of the night, -2 to -4).

Night and day	a	c	R ²
Knobbed night	-2.94	114,317	0.43
Knobbed day	-1.97	76,339	0.57
All night	-2.57	99,595	0.30
All day	-2.30	89,273	0.62
All whelk	a	c	R ²
-3 to -4	-6.29	244,162	0.89
0 to -2	-2.10	81,562	0.68
0 to +2	-1.49	57,705	0.40
+2 to +4	-3.18	123,233	0.79
Knobbed whelk	a	c	R ²
-3 to -4	-5.91	229,471	0.90
0 to -2	0.29	-11,214	0.01
0 to +2	2.54	-98,518	0.35
+2 to +4	0.89	-34,455	0.10

could be enhanced to support a supplemental fishery by collecting at night.

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Appendix 1. Number of individuals of whelk collected in relation to date, time, sunrise and sunset, day interval (four quadrants from sunrise to midday ranked 0 to 4, quadrants from midday to sunset ranked 4 to 0, quadrants from sunset to the middle of night ranked 0 to -4, and quadrants from middle of night to sunrise ranked -4 to 0), MLLW Mean Lower Low Water (NOAA, Beach Hammock), percentage of moon visible (US Naval Observatory), water and air temperature (thermometer at Dead Man Hammock).

Date	Start	End	Sunrise	Sunset	Light intensity	Tidal height	Low tide	Lunar phase	Water temp.	Air temp.	Knob.	Light.	Chan.	All whelk
M/D/Y	(h:min)	(h:min)	(h:min)	(h:min)	(-4 to 4)	(MLLW)	(h:min)	(% Visible)	(°C)	(°C)	(#)	(#)	(#)	(#)
2/27/2006	15:00	16:40	6:54	18:21	2.5	-0.37	13:41	0	13.5	14	16	3	0	19
2/28/2006	1:30	4:45	6:53	18:21	-3	-0.43	1:58	1	12.5	9	201	9	8	218
2/28/2006	14:00	16:20	6:53	18:21	3	-0.46	14:29	1	13	18.5	110	16	3	129
3/1/2006	2:40	4:45	6:52	18:22	-2.5	-0.46	2:49	4	13	11	64	2	8	74
3/1/2006	14:10	16:00	6:52	18:22	3	-0.46	15:15	4	14.5	23	69	9	1	79
3/2/2006	3:10	4:55	6:51	18:23	-2.5	-0.40	3:39	10	14	13	96	2	6	104
3/2/2006	14:35	16:15	6:51	18:23	2.5	-0.43	16:00	10	15.5	24	81	2	0	83
3/3/2006	3:45	5:25	6:49	18:24	-1.5	-0.27	4:29	19	15.5	16	82	0	3	85
3/3/2006	16:10	17:30	6:49	18:24	2	-0.30	16:46	19	16.5	14.5	64	1	0	65
3/4/2006	16:35	18:05	6:48	18:24	1.5	-0.15	17:33	28	15.5	11.5	70	3	3	76
3/5/2006	6:05	7:15	6:47	18:25	0	0.09	6:12	38	14	8	63	1	1	65
3/5/2006	17:30	18:35	6:47	18:25	1	0.00	18:24	38	15	13	19	1	1	21
3/6/2006	7:05	8:10	6:46	18:26	-1.5	0.24	7:12	50	14.5	12	33	1	4	38
3/13/2006	:20	2:20	6:37	18:31	-4	0.06	:55	99	18	18	132	8	7	147
3/13/2006	12:30	14:00	6:37	18:31	4	0.09	13:17	99	18.5	24.5	45	3	1	49
3/14/2006	:40	2:30	6:36	18:32	-3.5	0.03	1:36	100	18.5	18.5	130	1	6	137
3/14/2006	13:15	14:45	6:36	18:32	4	0.06	13:52	100	19	21	54	1	6	61
3/15/2006	1:20	3:05	6:35	18:32	-3.5	0.00	2:14	100	18	11.5	62	0	1	63
3/15/2006	13:30	14:35	6:35	18:32	4	0.03	14:25	100	17.5	18.5	19	2	0	21
3/16/2006	2:40	4:10	6:33	18:33	-2.5	0.00	2:51	97	17	10	25	0	0	25
3/16/2006	14:25	15:40	6:33	18:33	3	0.03	14:57	97	17	19.5	18	1	1	20
3/26/2006	23:05	:55	6:21	18:40	-4	-0.15	23:51	11	13.5	9	40	1	7	48
3/27/2006	11:40	13:00	6:19	18:41	4	-0.24	12:25	4	13.5	14.5	11	3	0	14
3/27/2006	:10	1:30	6:19	18:41	-4	-0.27	:48	1	13.5	11	26	1	2	29
3/28/2006	12:15	13:25	6:18	18:41	4	-0.34	13:14	1	14.5	19.5	8	2	0	10
3/29/2006	1:00	2:30	6:17	18:42	-3.5	-0.34	1:41	0	14.5	14.5	38	0	4	42
3/29/2006	13:10	14:30	6:17	18:42	4	-0.40	14:02	0	15.5	21.5	10	0	0	10
3/30/2006	1:45	3:15	6:15	18:43	-3.5	-0.34	2:33	2	15.5	15.5	22	1	4	27
3/30/2006	13:55	15:25	6:15	18:43	3.5	-0.40	14:28	2	16	17	8	0	2	10
3/31/2006	2:40	4:00	6:14	18:43	-2.5	-0.30	3:22	7	15.5	15.5	19	0	5	24
3/31/2006	14:55	16:20	6:14	18:43	2.5	-0.30	15:34	7	17.5	24	7	0	1	8
4/1/2006	3:30	5:00	6:13	18:44	-2	-0.18	4:10	14	17	16.5	14	0	1	15
4/1/2006	15:15	16:30	6:13	18:44	2	-0.18	16:19	14	18.5	23.5	7	0	0	7